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The impact of Enchytraeidae (Oligochaeta) on the pore structure of small microcosms

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The effect of Enchytraeidae (Oligochaeta) on the pore structure of a soil is determined by evaluating changes in the ratio of the minimum Ferret diameter to the maximum Ferret diameter (aspect ratio) of elongate pores. In small microcosms the burrowing activities of *Enchytraeus minutus* were followed during a 51 day period. The microcosms consisted of two glass plates with a bottom of plaster of Paris and sides of Plexiglass. The microcosms were filled with enchytraeid free, < 1 mm sieved soil. Two soil management treatments were simulated by the addition of rye litter to the surface or by incorporating it into the soil. Every 17 days series of photographs from the surface to a depth of 12 cm were taken. The negatives were analyzed on an image analysis system for pore characteristics. The ratio of the number of pores with an aspect ratio ≤ 0.5 to the total number of pores increased in the buried litter microcosms after 17 and 34 days. Through their burrowing activities enchytraeids caused a shift to more elongated pores in the buried litter microcosms. Consolidation of the soil counteracted the effects of enchytraeids at later times in the experiment.

1. Introduction

Pore space in soils, including its size distribution and shape affects many important phenomena including storage and movement of water, nutrients and gases, and ease of root penetration. Pore measurements are increasingly used to characterize soil structure because it is the size, shape and continuity of pores that affect many of the important processes in soils (Lawrence 1977, Elliott & Coleman 1988).

Most image analysis programs provide the user with a large choice of parameters that can be measured. The shape factor (Area/Perimeter^2) is often used to distinguish rounded, vughy and planar voids. Bisdom & Schoonderbeek (1983), however, have shown that one shape factor can represent pores with a number of different shapes. They concluded that the ratio of the minimum Ferret diameter to the maximum Ferret diameter (aspect ratio) was a better indicator of pore shape. They suggested that values of the aspect ratio of 0.5 or less would identify elongate pores.

Soil organisms are partly responsible for the formation of soil structure yet are restricted by it as well. The faunal influence on pore structure can be divided into the following aspects: a) enlargement of pores, by applying pressure or transporting soil material; b) reduction of pore sizes, for instance, by the filling of pores, or as an effect of external pressure; and c) formation of new pores by burrowing (Didden 1990). Didden (1990) showed that Enchytraeidae (Oligochaeta) increased the pore continuity and raised the volume of pores corresponding to their body size. Van Vliet et al. (1993) showed that enchytraeids increased the porosity in microcosms after 17 days. At later times, the porosity of the microcosms decreased to levels below the starting values. Enchytraeids may have refilled the pores with their excrements and, due to the high moisture content of the microcosms (36%), may have decreased the aggregate stability by passage of the soil through their gut. The vertical distribution of enchytraeids through a soil is strongly related to the placement of residue. In no-tillage systems more enchytraeids are found in the upper soil layer, while in plowed systems enchytraeids are more evenly distributed over the soil profile (Didden 1993). Therefore the effect of enchytraeids on soil structure might be related to residue placement.

The objective of this study was to determine the influence of enchytraeids on the aspect ratio of pores in a soil low in organic matter with different residue placements. Analyses were focused on the elongated pores (i.e., with an aspect ratio ≤ 0.5).

2. Methods

Enchytraeids were incubated in microcosms consisting of 2 glass sheets (18 × 27.5 cm) which were held apart by a 0.3 cm thick layer of Plaster of Paris at the bottom (ratio of plaster (g) to water (ml): 1.9:1) and Plexiglas at the sides (van Vliet et al. 1993).

Two soil management treatments were simulated by the addition of 0.8 g of rye (*Secale cereale* L.) to the surface (SL, surface litter) or by incorporating it into the soil before the soil was added to the microcosms (BL, buried litter). The rye was ground smaller than 0.2 mm in size so as to prevent the organic matter – soil mixture from becoming too porous. Each microcosm was filled from the top with 65 g of air-dried soil aggregates smaller than 1 mm. The soil was a sandy clay loam surface horizon from a clayey, kaolinitic, thermic Typic Kanhapludult, with a carbon content of 1.6%, 16% silt and 13% clay. Further soil characteristics and the pre-treatment of the soil are described in van Vliet et al. (1993). The litter layer in the SL treatment was approximately 1 cm thick. The bulk density in the microcosms was 1.20 and 1.25 g/cm^3 for the BL and the SL treatments, respectively. The microcosms were placed in a pan with 0.1 to 0.3 cm deep water, and the soil in the microcosms wetted from below through the capillary action of the plaster and the soil. Because of this set-up the soil in the microcosms remained wet (36%) during the experiment.

Each litter placement treatment consisted of 6 microcosms. To 3 of the 6 microcosms twenty enchytraeids (*Enchytraeus minutus* Nielsen & Christensen 1961) were added at the top of the soil (for the BL treatment) or litter layer (for the SL treatment). The organisms had an average length of 6 mm and width of 0.3 mm. The microcosms were stored in a dark room with the temperature fluctuating between 20° and 24°C, which simulates the temperatures in late spring or early fall in Georgia when large numbers of enchytraeids can be found in the field.

Aspect ratios (minimum / maximum Ferret diameter) of the soil pores were measured before the addition of the enchytraeids (T0) and after 51 days (T3). For the microcosms containing enchytraeids, aspect ratios of pores were also determined after 17 (T1) and 34 (T2) days. To determine porosity characteristics, black and white photographs (Kodak TMX 100 film) were taken through a stereomicroscope at a magnification of 10×. Two series of photographs, each photograph encompassing 1 cm vertically, were taken from the surface to a depth of 12 cm. Using an Olympus Cue-2 digital image analyzing system the negatives were analyzed for the following pore characteristics: area, aspect ratio, orientation, perimeter and shape factor. An area of 52 mm^2 was analyzed on each negative and small objects (smaller than 2 × 2 pixels, 0.0012 mm^2) were removed from the image. Aspect ratios per cm for the 2 series and for the 1–4, 5–8 and 9–12 cm depth increments were combined for subsequent analysis. For each treatment and each time period frequency distributions of the number of pores with an aspect ratio ≤ 0.5 were made. The following grouping was used: 0–0.05, >0.05–0.1, >0.1–0.15, etc. up to >0.45 to 0.5. Differences between the different distributions were analyzed using a Kolmogorov-Smirnov two sample test (Sokal & Rohlf 1981).

3. Results

No significant differences in frequency distributions of the aspect ratio were found between the enchytraeid and non-enchytraeid treatments after 51 days (data not shown).

Table 1 shows the ratio of the number of elongate pores (aspect ratio ≤ 0.5) and the total number of pores found in the different treatments, at the different depth increments at the different time periods. From T0 to T2 the ratio in the BL with enchytraeids treatment increased significantly in all 3 depth increments, indicating that more of the pores were elongated. From T2 to T3 in all depth

Table 1. The ratio of the number of pores with an aspect ratio ≤ 0.5 and the total number of pores found in the different treatments at 3 depths at different time periods (n = 3, standard errors in parentheses). Significant changes in the ratio per treatment and per depth are indicated by different letters (P < 0.05).

Depth	Time	Buried litter + Enchy	Buried litter – Enchy	Surface litter + Enchy	Surface litter – Enchy
1-4 cm:	T0	0.41 a (0.01)	0.42 a (0.02)	0.42 a (0.02)	0.45 a (0.01)
	T1	0.46 ab (0.02)		0.42 a (0.01)	
	T2	0.49 b (0.02)		0.44 a (0.004)	
	T3	0.45 ab (0.01)	0.44 a (0.02)	0.45 a (0.01)	0.42 a (0.02)
5–8 cm:	T0	0.40 a (0.02)	0.42 a (0.01)	0.43 ab (0.01)	0.45 a (0.02)
	T1	0.47 b (0.01)		0.40 b (0.003)	
	T2	0.51 b (0.01)		0.45 a (0.001)	
	T3	0.46 ab (0.01)	0.43 a (0.02)	0.42 ab (0.01)	0.42 a (0.01)
9–12 cm:	T0	0.42 a (0.01)	0.39 a (0.01)	0.45 a (0.03)	0.44 a (0.02)
	T1	0.46 ab (0.01)		0.43 a (0.04)	
	T2	0.48 b (0.01)		0.48 a (0.02)	
	T3	0.45 ab (0.02)	0.39 a (0.004)	0.50 a (0.06)	0.39 a (0.01)

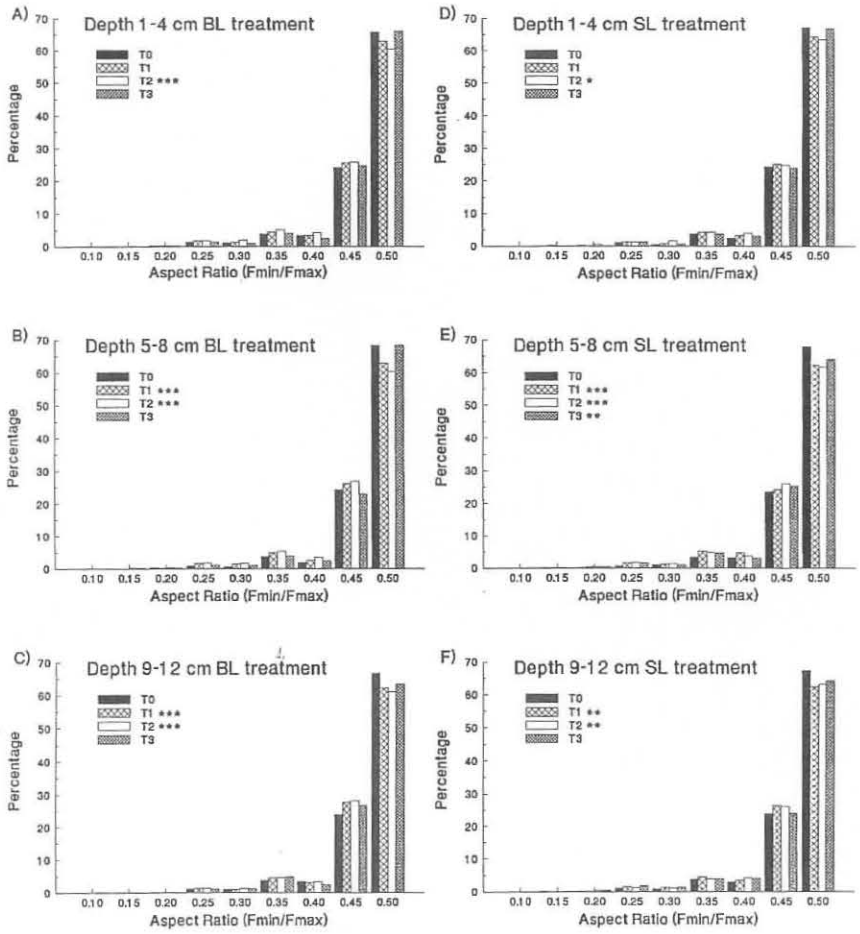

Fig. 1. Frequency distributions of the aspect ratios of the pores at different time periods (T0, T1, T2 and T3) at 3 depth increments for the buried litter placement (BL) (A, B and C) and the surface litter placement (SL) treatment (D, E and F). Asterisks denote a significant difference between the frequency distribution at Tx and at T0 (* = significant at $P < 0.1$; ** = significant at $P < 0.05$; *** = significant at $P < 0.01$).

Table 2. Significant differences (*P*-values, two-sample Kolomogorov-Smirnov test) for the frequency distributions of the aspect ratio between time periods for the BL and SL microcosms with enchytraeids.

Times	Buried litter Depth increment 1–4	5–8	9–12	Surface litter Depth increment 1–4	5–8	9–12
T0–T1	n.s.	0.01	0.01	n.s.	0.01	0.05
T0–T2	0.01	0.01	0.01	0.1	0.01	0.05
T0–T3	n.s.	n.s.	n.s.	n.s.	0.05	n.s.
T1–T2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
T1–T3	0.01	0.01	n.s.	0.01	0.01	0.01
T2–T3	0.01	0.01	n.s.	n.s.	n.s.	n.s.

increments the ratio decreased (although not significantly). In the SL treatments with and without enchytraeids no significant changes in the ratio occurred, except in the 5–8 cm depth increment from T1–T2.

Table 2 shows the results of the statistical analysis of the aspect ratio frequency distributions. The T0 and T3 frequency distributions were not significantly different in the BL treatment and only significantly different at the 5–8 cm depth in the SL treatment. The frequency distributions significantly changed from T0–T1 at the 5–8 cm and the 9–12 cm depth increments in both treatments. At T2, 34 days after the start of the experiment, in both treatments and at all depths the frequency distributions were significantly different from the distributions at T0. Fig. 1 shows the aspect ratio frequency distributions for both treatments

and all depth increments. At T1 and T2 (compared to T0), a shifting towards smaller ratio factors occurred at all depth increments in both treatments.

4. Discussion

Simultaneously with an increase in the ratio of the number of elongated pores and the total number of pores, a shift in the frequency distributions of the aspect ratios was found at T1 and T2 for the BL treatment. At these times, aspect ratios were smaller, suggesting that the pores were more elongated than in the initial soil.

Van Vliet et al. (1993) noticed after 17 days an increase in porosity in all depth increments in the BL microcosms with enchytraeids, whereas the non-enchytraeid controls showed a decline in porosity suggesting consolidation of the soil. Through their burrowing activities enchytraeids caused an increase in porosity and a shift to more elongate pores. At T2 still more of the pores were elongated in the enchytraeid treatment, but Van Vliet et al. (1993) found no increase in the total porosity at T2 compared to the porosity at T0. The effect of enchytraeids on the soil porosity may have been counteracted by consolidation of the soil and by infilling of the pores with excrements. Furthermore, the decrease in the ratio of elongated to the total number of pores, from T2 to T3 in the BL treatment with enchytraeids may be attributable to an increased consolidation of the soil due to enchytraeid activity. The constantly high moisture content of the soil (36%) and the egestion of the soil by the enchytraeids may have destabilized the soil aggregates. Under field conditions the stability of the enchytraeid fecal pellets might be increased by ageing and drying as observed for earthworm casts (Shipitalo & Protz 1988, Marinissen & Dexter 1990).

Although no significant changes were found in the ratio of the number of elongated to the total number of pores in the SL microcosms at the 1–4 and 9–12 cm depth increments, a shift to more elongated pores was found at T1 and T2. Van Vliet et al. (1993) found a significant increase in porosity at the 1–4 cm depth increment at T1 and T2 due to enchytraeid activity, while in the non-enchytraeid controls the total porosity decreased. Approximately 85% of the enchytraeids in the SL microcosms were found in the litter and in the 1–4 cm depth increment. The new pores formed by the enchytraeids in the 1–4 cm depth increment, may have been elongated initially but infilling with excrements and consolidation may have masked their shape. Enchytraeid activity at the 5–8 and 9–12 cm depth increments may have led to a change in pore shape (i.e., aspect ratio) but because no change in the porosity was measured, their activity may have been counteracted by consolidation of the soil. The absence of organic matter in the soil might have led to the decreased stability of the pores in the SL microcosms. Therefore we hypothesize that the pores made by enchytraeids are more stable in the presence of incorporated organic matter. Enchytraeids might therefore have a greater impact on soil structure in plowed, well mixed soils than in no-tillage soil.

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